Amer. Malac. Bull. 30(1): 19–38 (2012)

The genera of Pleurobemini (Bivalvia: Unionidae: Ambleminae)

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Abstract: The unionid tribe Pleurobemini is diverse but poorly-understood phylogenetically. Current classification recognizes two highly diverse genera, *Elliptio* Rafinesque, 1819 and *Pleurobema* Rafinesque, 1820, besides the moderately diverse *Fusconaia* Simpson, 1900, and several genera with one to three species. However, classification at the species and genus level has been problematic. Molecular data and re-examination of shell morphology and anatomy indicate new groupings of these taxa. Several genera proposed by early workers such as Rafinesque and Swainson are available, but are poorly-characterized and are often overlooked. We analyzed two mitochondrial genes, *coxi* and *nad1*, for 50 species assigned to Pleurobemini, including the type species of each genus and as many other species as possible. Although the majority of studied species in *Elliptio*, *Pleurobema*, and *Fusconaia* show close affinities to the respective type species, the affinities of others are problematic. Genera or subgenera such as *Eurynia* Rafinesque, 1819, *Sintoxia* Rafinesque, 1820, and *Pleuronaia* Frierson, 1927, generally regarded as subjective synonyms, apply to some clades. Other clades or unaffiliated species have no available name. *Quincuncina burkei* (Walker, 1922), the type of the genus *Quincuncina* Ortmann, 1922, is assigned to *Fusconaia* Simpson, 1900. *Fusconaia apalachicola* (Williams and Fradkin, 1999), *F. ebenus* (Lea, 1831), *F. rotulata* (Wright, 1899) (also listed as *Obovaria rotulata*), *F. succissa* (Lea, 1852), *Cyclonaias tuberculatus* (Rafinesque, 1820), *Uniomerus* Conrad, 1853, and the *Quincuncina infucata* (Conrad, 1834) complex are all excluded from Pleurobemini. The first three are placed in the new genus *Reginaia* Campbell and Lydeard; *Uniomerus* Conrad, 1853 is assigned to Quadrulini; and the remainder belong in the *pustulosa* Lea, 1831 group of Quadrulini (genus *Rotundaria* Rafinesque, 1820).

Key words: systematics, nomenclature, freshwater mussels, Unioniformes

North America has the highest diversity of freshwater mussels (Unionoida) in the world, with > 300 species and > 50 genera. Current classification (Graf and Cummings 2007) assigns most of these taxa to the subfamily Ambleminae, which in turn is divided into the tribes Amblemini, Gonidini, Lampsilini, Pleurobemini, and Quadrulini. Recognition of Pleurobemini has developed gradually. Hannibal (1912) first recognized the Pleurobemini as a distinct group (as a subfamily), but the composition of the tribe varies among authors. Many workers allied or even synonymized it with the Old World tribe Unionini. Simpson (1914) also placed Margaritiferidae in this group. Most pre-cladistic morphology- and anatomy-based classifications of the Unionoida placed great weight on a single character such as gill modifications, breeding season, beak sculpture, or hinge, depending on the author. This neglected evidence for homoplasy, and also led to the use of symplesiomorphies as diagnostic features in classification. At the tribe level, *Fusconaia* Simpson, 1900 was grouped with *Quadrula* Rafinesque, 1820 rather than with Pleurobemini in the classifications of Simpson (1900, 1914) and Heard and Guckert (1971) due to its generally tetragenous brooding. Likewise, sculptured shells such as *Plethobasus* Simpson, 1900 and *Quincuncina* Ortmann, 1922 frequently were assigned to Quadrulini. Modell (1964) and others assigned the thin-shelled, weakly dentate *Hemistena* Rafinesque, 1820 to the alasmidontines (now considered a synonym of anodontines, Graf and Cummings 2007). Detailed anatomy (Ortmann 1911, Heard and Guckert 1971) showed that the Pleurobemini were not congeneric with Old World *Unio* Philipsson, 1788, but they often remained assigned to the same tribe or subfamily. Molecular analyses, starting with Davis and Fuller (1981), led to the recognition of Pleurobemini as a distinct member of the Ambleminae, only distantly related to *Unio*.

Within Pleurobemini, most species are assigned to *Elliptio* Rafinesque, 1820, *Pleurobema* Rafinesque, 1820, and *Fusconaia* Simpson, 1900, with *Elliptio* dominating the Atlantic drainage and *Pleurobema* and *Fusconaia* dominating the Gulf of Mexico drainages. Other genera sometimes assigned to Pleurobemini have one to four recognized species. Currently recognized genera include *Cyclonaias* Pilsbry, 1922, *Elliptoideus* Frierson, 1927, *Hemistena* Rafinesque, 1820, *Lexingtonia* Ortmann, 1914, *Plectomerus* Conrad, 1853, *Plethobasus*, *Popenaias* Frierson, 1927, *Quincuncina*, and *Uniomerus* Conrad, 1853. However, many of the poorly-characterized genera proposed by Rafinesque (1819, 1820, 1831, 1832) and Swainson (1840) have not been re-examined in light of modern data and usage.

Several species have been classified in different genera by different authors, especially the more poorly-known species from southern U. S. drainages. This reflects the general lack

of obvious characters such as shell sculpture or specialized host-attraction structures that facilitate division of Quadrulini and Lampsilini into genera. Additionally, many of these species had not received much anatomical study. For example, *Pleurobema beadleianum* (Lea, 1861) has been placed in *Elliptio* and *Fusconaia* (Vidrine 1993), *Fusconaia rotulata* (Wright, 1899) has also been assigned to *Obovaria* (Williams *et al.* 2008), *Pleurobema collina* (Conrad, 1837) has been placed in *Alasmidonta*, *Canthyria*, *Lexingtonia*, and *Fusconaia* (Johnson 1970) and closely resembles *Elliptio steinstanana* Johnson and Clarke, 1983, and *Pleurobema riddellii* (Lea, 1862) has also been placed in *Fusconaia* (Vidrine 1993). Some authors make their genus assignments even more confusing by putting a formerly used genus in parentheses after the current genus, *e.g.* "*Villosa* (*Micromya*) *lienosa*". This format is standard for indicating a subgenus and should not be used for outdated genera; instead, a format such as "*Villosa lienosa* (formerly *Micromya*)" makes the intent clear (ICZN 1999, Recommendation 6A).

To provide new phylogenetic data, we used mitochondrial DNA sequencing. Genetic data provide an independent line of evidence for taxonomy, particularly useful when morphological and anatomical studies have had so much difficulty in confidently delimiting evolutionarily significant units. Although molecular data are not inherently superior to morphological data, they are of particular value when morphological variation is either slight or difficult to characterize, such as the subtle shape differences among many species in Pleurobemini. As Graf and Cummings (2006) point out, some published sequences are problematic, and different analyses of the same data can yield different results. However, additional sequences provide a check on previous work, and increasing both the number of taxa and the amount of data per taxon generally improves the robustness of phylogenetic results. Mitochondrial DNA can potentially follow a different evolutionary course from the main genetic heritage of a species, *e.g.*, through hybridization and introgression. But in freshwater mussels, the importance of distinct male and female mitochondrial lineages in the overall biology of the mussel makes discordant evolution of the mitochondria much less likely (Breton *et al.* 2011). A few species of Pleurobemini have been included in almost every previous molecular study on Ambleminae; several include multiple species (Lydeard *et al.* 2000, Kandl *et al.* 2001, Campbell *et al.* 2005, Burdick and White 2007, Campbell *et al.* 2008, and Campbell and Lydeard 2012). Representatives of other tribes were used as outgroups. We sequenced portions of two mitochondrial genes that had proven useful for species-level studies on unionids: cytochrome oxidase I (*cox1*) (Roe and Lydeard 1998) and NADH dehydrogenase I (*nad1*) (Buhay *et al.* 2002; Serb, Buhay *et al.* 2003). We also tried nuclear ITS1 sequences. Although it has worked for other unionids, ITS1 failed to give clear resolution within Pleurobemini (Campbell *et al.* 2008).

Our goal in this paper is to review the nomenclaturally available genera of Pleurobemini and to compare the nomenclature with the clades generated by analyses of molecular data for these taxa.

MATERIALS AND METHODS

We included sequences for 42 unambiguous species of Pleurobemini and 10 additional species that have been assigned to Pleurobemini by some authors, including the type species of all currently recognized genera and all available types of other genera. Outgroups were selected to represent the other tribes of Ambleminae. Table 1 lists the sequences generated in the present study, and Table 2 gives collection information for specimens with new data.

DNA extraction used either CTAB and chloroform-isoamyl alcohol protocols (Winnepenninckx *et al.* 1993) or Qiagen DNA extraction kits. The ITS1 region and portions of the *cox1* and *nad1* genes were amplified. Primers for *cox1* were 5′-GTTCCACAAATCATAAGGATATTGG-3′ and 5′-TACACCTCAGGGTGACCAAAAAACCA-3′, adapted from Folmer *et al.* (1994); primers for *nadh1* were 5′-TGGCA GAAAAGTGCATCAGATTTAAGC-3′ and 5′-GCTATTAGTA GGTCGTATCG-3′ (Buhay *et al.* 2002, Serb and Lydeard 2003); and primers for ITS1 were 5'-AAAAAGCTTCCG TAGGTGAACCTGCG-3' and 5'-AGCTTGCTGCGTTCTT CATCG-3' (King *et al.* 1999). For members of the Quadrulini, the primer LoGlyR (5'-CCTGCTTGGAAGGCAAGTGT ACT-3') (Serb, Buhay *et al.* 2003) often worked better as a reverse primer for *nadh1*. *Uniomerus* amplified with it but not with the above reverse primer (which also failed to amplify for Sommer (2007)). The forward primer UNIOCOII.2 from Walker *et al.* (2007) and/or the reverse primer HCOout (CCAGGTAAAATTAAAATATAAACTTC, Carpenter and Wheeler 1997) provided good amplification for *cox1* for some species. PCR cycles were: 92 °C 2 min; 92 °C 40 s, 40 °C 40 s, 72 °C 90 s 5×; 92 °C 40 s, 50 °C 40 s, 72 °C 90 s 25×; 72 °C 10 min; hold 4 °C. PCR products were purified using Qiagen QIAquick PCR purification kits and, if necessary, Qiagen gel extraction kits. Cycle sequencing used ABI Big Dye Terminator kits with thermal cycle parameters of 1 °C per second ramp speed, starting with 1 min at 96 °C followed by 26 cycles of 96 °C for 10 s, 49 °C for 5 s, and 60 °C for 4 min, then 10 min at 60 °C and hold at 4 °C. The cycle sequencing products were purified with Qiagen DyeEx kits and then run on an automated sequencer.

The results for each strand were compared and aligned using BioEdit (Hall 1999). We analyzed the sequences with TNT (Goloboff *et al.* 2008). Maximum parsimony analyses

Table 1. Sequences used. UAUC and UA are different versions of the University of Alabama catalog.

Taxon	Source	Accession	Gene
Amblema elliottii (Lea, 1856)	Campbell *et al.* 2005	AY654991	*cox1*
Amblema elliottii	Campbell *et al.* 2005	AY655086	*nad1*
Amblema plicata (Say, 1817)	Chapman, Piontkivska *et al.* 2008	EF033258	*cox1*
Amblema plicata	Serb, Buhay *et al.* 2003	AY158796	*nad1*
Dromus dromas (Lea, 1834)	Campbell *et al.* 2005	AY654993	*cox1*
Dromus dromas	UAUC3156	JF326439*	*nad1*
Elliptio arca	Campbell *et al.* 2005	AY654995	*cox1*
Elliptio arca	Campbell *et al.* 2005	AY655093	*nad1*
Elliptio arctata	Campbell *et al.* 2008	DQ383427	*cox1*
Elliptio arctata	UAUC3496	JF326440*	*nad1*
Elliptio complanata	Gangloff *et al.* in review	EU448172	*cox1*
Elliptio complanata	Kneeland and Rhymer 2007	EF446099	*nad1*
Elliptio crassidens	Campbell *et al.* 2008	DQ383428	*cox1*
Elliptio crassidens	Campbell *et al.* 2005	AY613788	*nad1*
Elliptio mcmichaeli	Gangloff *et al.* in review	EU377573	*cox1*
Elliptio mcmichaeli	UA3088	JF326441*	*nad1*
Elliptio pullata	Gangloff *et al.* in review	EU377571	*cox1*
Elliptio pullata	Gangloff *et al.* in review	EU380666	*nad1*
Elliptio purpurella	Gangloff *et al.* in review	EU377574	*cox1*
Elliptio purpurella	UA3569	JF326442*	*nad1*
Elliptio shepardiana	Gangloff *et al.* in review	EU448252	*nad1*
Elliptio (*Eurynia*) *dilatata*	Graf and Ó Foighil 2000	AF156507	*cox1*
Elliptio dilatata	Campbell *et al.* 2005	AY613789	*nad1*
Elliptoideus sloatianus	Campbell *et al.* 2005	AY613821	*cox1*
Elliptoideus sloatianus	Campbell *et al.* 2005	AY613790	*nad1*
Epioblasma rangiana (Lea, 1838)	new-clip from Virginia Tech	JF326432*	*cox1*
Epioblasma rangiana	Zanatta and Murphy 2006	DQ220720	*nad1*
Fusconaia burkei	Lydeard *et al.* 2000	AF232804	*cox1*
Fusconaia burkei	Serb, Buhay *et al.* 2003	AY158793	*nad1*
Fusconaia cerina	Campbell *et al.* 2005	AY613823	*cox1*
Fusconaia cerina	Campbell *et al.* 2005	AY613792	*nad1*
Fusconaia cor	Campbell *et al.* 2005	AY654997	*cox1*
Fusconaia cor	Campbell *et al.* 2005	AY655096	*nad1*
Fusconaia cuneolus	Campbell *et al.* 2005	AY654998	*cox1*
Fusconaia cuneolus	Campbell *et al.* 2005	AY655097	*nad1*
Fusconaia escambia	Lydeard *et al.* 2000	AF232816	*cox1*
Fusconaia escambia	Campbell and Lydeard 2011	HM230413*	*nad1*
Fusconaia flava	Bogan and Hoeh 2000	AF231733	*cox1*
Fusconaia flava	Campbell *et al.* 2005	AY613793	*nad1*
Fusconaia masoni	Campbell and Lydeard 2011	HM230371*	*cox1*
Fusconaia masoni	Campbell and Lydeard 2011	HM230415*	*nad1*
Fusconaia ozarkensis	Campbell and Lydeard 2011	HM230373*	*cox1*
Fusconaia ozarkensis	Campbell and Lydeard 2011	HM230416*	*nad1*
Fusconaia subrotunda	Campbell *et al.* 2005	AY613824	*cox1*
Fusconaia subrotunda	Campbell *et al.* 2005	AY613794	*nad1*
Glebula rotundata (Lamarck, 1819)	Chapman, Piontkivska *et al.* 2008	EF033264	*cox1*
Glebula rotundata	Campbell *et al.* 2005	AY613795	*nad1*
Hemistena lata	Campbell *et al.* 2005	AY613825	*cox1*
Hemistena lata	Campbell *et al.* 2005	AY613796	*nad1*
Lampsilis ovata (Say, 1817)	Chapman, Piontkivska *et al.* 2008	EF033262	*cox1*
Lampsilis ovata	Campbell *et al.* 2005	AY613797	*nad1*
Lampsilis virescens (Lea, 1858)	new clip from Alabama Aquatic Biodiversity Center	JF326433*	*cox1*

Table 1. (Continued)

Taxon	Source	Accession	Gene
Lampsilis virescens	new clip from Alabama Aquatic Biodiversity Center	JF326443*	*nad1*
Lemiox rimosus (Rafinesque, 1831)	Campbell and Lydeard 2011	HM230406*	*cox1*
Lemiox rimosus	Campbell and Lydeard 2011	HM230417*	*nad1*
Obliquaria reflexa (Rafinesque, 1820)	Chapman, Piontkivska *et al.* 2008	EF033254	*cox1*
Obliquaria reflexa	Campbell *et al.* 2005	AY655008	*nad1*
Obovaria jacksoniana	Campbell *et al.* 2005	AY655009	*cox1*
Obovaria jacksoniana	Campbell *et al.* 2005	AY655109	*nad1*
Obovaria (*Pseudoon*) *olivaria*	Chapman, Piontkivska *et al.* 2008	EF033267	*cox1*
Obovaria (*Pseudoon*) *olivaria*	Campbell and Lydeard 2011	HM230420*	*nad1*
Plectomerus dombeyanus (Valenciennes, 1827)	Chapman, Piontkivska *et al.* 2008	EF033252	*cox1*
Plectomerus dombeyanus	Campbell *et al.* 2005	AY655110	*nad1*
Plethobasus cyphyus	Campbell *et al.* 2005	AY613828	*cox1*
Plethobasus cyphyus	Campbell *et al.* 2005	AY613799	*nad1*
Pleurobema athearni	Campbell *et al.* 2005	AY655015	*cox1*
Pleurobema athearni	Campbell *et al.* 2005	AY655114	*nad1*
Pleurobema beadleianum	Campbell *et al.* 2008	DQ383429	*cox1*
Pleurobema beadleianum	Campbell *et al.* 2008	AY613800	*nad1*
Pleurobema clava	Campbell *et al.* 2005	AY655013	*cox1*
Pleurobema clava	Campbell *et al.* 2005	AY613802	*nad1*
Pleurobema collina	Campbell *et al.* 2005	AY613830	*cox1*
Pleurobema collina	Campbell *et al.* 2005	AY613803	*nad1*
Pleurobema decisum	Campbell *et al.* 2005	AY613832	*cox1*
Pleurobema decisum	Campbell *et al.* 2005	AY655112	*nad1*
Pleurobema furvum	Campbell *et al.* 2005	AY613833	*cox1*
Pleurobema furvum	Campbell *et al.* 2005	AY613806	*nad1*
Pleurobema georgianum	Campbell *et al.* 2005	AY613834	*cox1*
Pleurobema georgianum	Campbell *et al.* 2005	AY613807	*nad1*
Pleurobema hanleyianum	Campbell *et al.* 2005	AY613836	*cox1*
Pleurobema hanleyianum	Campbell *et al.* 2005	AY655115	*nad1*
Pleurobema oviforme	Campbell *et al.* 2005	AY655017	*cox1*
Pleurobema oviforme	Campbell *et al.* 2005	AY613810	*nad1*
Pleurobema perovatum	new Wilson Creek	*JN180999	*cox1*
Pleurobema perovatum	Campbell *et al.* 2005	AY613811	*nad1*
Pleurobema pyriforme	Campbell *et al.* 2005	AY613839	*cox1*
Pleurobema pyriforme	Campbell *et al.* 2005	AY613812	*nad1*
Pleurobema stabile	Campbell *et al.* 2008	AY613842	*cox1*
Pleurobema stabile	Campbell *et al.* 2008	AY613816	*nad1*
Pleurobema strodeanum	Campbell *et al.* 2005	AY613843	*cox1*
Pleurobema strodeanum	Campbell *et al.* 2005	AY613817	*nad1*
Pleurobema taitianum	Campbell *et al.* 2005	AY613844	*cox1*
Pleurobema taitianum	Campbell *et al.* 2005	AY613818	*nad1*
Pleurobema (*Sintoxia*) *cordatum*	Campbell *et al.* 2005	AY613831	*cox1*
Pleurobema (*Sintoxia*) *cordatum*	Campbell *et al.* 2005	AY613804	*nad1*
Pleurobema (*Sintoxia*) *riddellii*	specimen 186	JF326434*	*cox1*
Pleurobema (*Sintoxia*) *riddellii*	specimen 186	JF326444*	*nad1*
Pleurobema (*Sintoxia*) *rubrum*	Campbell *et al.* 2005	AY613841	*cox1*
Pleurobema (*Sintoxia*) *rubrum*	UAUC529	JF326445*	*nad1*
Pleurobema (*Sintoxia*) *sintoxia*	Graf and Ó Foighil 2000	AF156509	*cox1*
Pleurobema (*Sintoxia*) *sintoxia*	Campbell *et al.* 2005	AY613815	*nad1*
Pleuronaia barnesiana	Campbell *et al.* 2005	AY613822	*cox1*
Pleuronaia barnesiana	Campbell and Lydeard 2011	HM230418*	*nad1*
Pleuronaia dolabelloides	Campbell *et al.* 2005	AY613827	*cox1*

Table 1. (Continued)

Taxon	Source	Accession	Gene
Pleuronaia dolabelloides	Campbell *et al.* 2005	AY613798	*nad1*
Pleuronaia gibbera	Campbell *et al.* 2005	AY613808	*nad1*
Pleuronaia gibbera	Campbell *et al.* 2008	DQ383432	*cox1*
Popenaias popeii	Campbell *et al.* 2005	AY655020	*cox1*
Popenaias popeii	Campbell *et al.* 2005	AY655118	*nad1*
Potamilus alatus	Bogan and Hoeh 2000	AF231752	*cox1*
Potamilus alatus	Campbell *et al.* 2005	AY655119	*nad1*
Potamilus capax (Green, 1832)	Roe and Lydeard 1998	AF049513	*cox1*
Potamilus capax	UAUC36	JF326446*	*nad1*
Quadrula nobilis	Lydeard *et al.* 2000	AF232823	*cox1*
Quadrula nobilis	new specimen, Sucarnochee River	JF326447*	*nad1*
Quadrula quadrula	Chapman, Piontkivska *et al.* 2008	EF033268	*cox1*
Quadrula quadrula	Breton *et al.* 2009	FJ809750	*nad1*
Quadrula rumphiana (Lea, 1852)	Campbell and Lydeard 2011	HM230409*	*cox1*
Quadrula rumphiana	Campbell and Lydeard 2011	HM230421*	*nad1*
Reginaia ebenus	Campbell *et al.* 2005	AY654999	*cox1*
Reginaia ebenus	Campbell and Lydeard 2011	HM230422*	*nad1*
Reginaia rotulata	Lydeard *et al.* 2000	AF232813	*cox1*
Reginaia rotulata	Serb, Buhay *et al.* 2003	AY158799	*nad1*
Rotundaria infucata	Lydeard *et al.* 2000	AF232806	*cox1*
Rotundaria infucata	Campbell *et al.* 2005	AY655121	*nad1*
Rotundaria kleiniana	Lydeard *et al.* 2000	AF232809	*cox1*
Rotundaria kleiniana	Serb, Buhay *et al.* 2003	AY158795	*nad1*
Rotundaria pustulosa	Henley *et al.* 2006	DQ640237	*nad1*
Rotundaria refulgens (Lea, 1868)	Chapman, Piontkivska *et al.* 2008	EF033269	*cox1*
Rotundaria refulgens	Serb, Buhay *et al.* 2003	AY158788	*nad1*
Rotundaria succissa	Lydeard *et al.* 2000	AF232820	*cox1*
Rotundaria succissa	Serb, Buhay *et al.* 2003	AY158792	*nad1*
Rotundaria tuberculata	Campbell and Lydeard 2011	HM230410*	*cox1*
Rotundaria tuberculata	Campbell *et al.* 2005	AY655088	*nad1*
Theliderma metanevra	new specimen, Cahaba River	JF326435*	*cox1*
Theliderma metanevra	new specimen, Cahaba River	JF326448*	*nad1*
Toxolasma lividum (Rafinesque, 1831)	new specimen, Tennessee River	JF326436*	*cox1*
Toxolasma lividum	new specimen, Tennessee River	JF326449*	*nad1*
Tritogonia verrucosa (Rafinesque, 1820)	Graf and Cummings 2006	DQ191413	*cox1*
Tritogonia verrucosa	Serb, Buhay *et al.* 2003	AY158791	*nad1*
Uniomerus declivis	Campbell *et al.* 2005	AY613846	*cox1*
Uniomerus declivis	UAUC3290	JF326450*	*nad1*
Uniomerus tetralasmus	new specimen, Hale County, Alabama	JF326437*	*cox1*
Uniomerus tetralasmus	new specimen, Hale County, Alabama	JF326451*	*nad1*
Venustaconcha ellipsiformis (Conrad, 1836)	Chapman, Piontkivska *et al.* 2008	EF033260	*cox1*
Venustaconcha ellipsiformis	Zanatta and Murphy 2006	DQ220722	*nad1*
Venustaconcha ellipsiformis 2	Campbell *et al.* 2005	AY655026	*cox1*
Venustaconcha ellipsiformis 2	Campbell *et al.* 2005	AY655126	*nad1*
Venustaconcha pleasii (Marsh, 1891)	UAUC3520, 3525(identical)	JF326438*	*cox1*
Venustaconcha pleasii	UAUC3520	JF326452*	*nad1*
Villosa fabalis (Lea, 1831)	Zanatta and Murphy 2006	DQ220726	*cox1*
Villosa fabalis	Zanatta and Murphy 2006	DQ220723	*nad1*

* indicates new sequences.

Table 2. Collection data for new material

Taxon	Collection #	Locality	Collector
Dromus dromas	UAUC3156	36.5756°N, 83.3664°W Powell River at McDowell Shoal, Hancock County, Tennessee	unknown
Elliptio arctata	UAUC3496	33.1853°N, 87.0002°W, Cahaba River at Booth's Ford, Shelby County, Alabama	P. Johnson
Elliptio mcmichaeli	UAUC3088	30.7773°N, 85.8497°W, Choctawhatchee River at U.S. Highway 90, Holmes County, Florida	Blalock, Hill, and Lewis
Elliptio purpurella	UAUC3569	31.0847°N, 85.1942°W, Rocky Creek at CR8, Houston County, Alabama	Campbell, Clark, Chesser
Epioblasma rangiana	clip from Virginia Tech	Allegheny River at Hunter Station Bridge, Venango County, Pennsylvania	Virginia Tech
Lampsilis virescens	clip from Alabama Aquatic Biodiversity Center	Estill Fork, Paint Rock River, Jackson County, Alabama	P. Johnson
Potamilus capax	UAUC36	35.5872°N, 90.4397°W, Iron Mines Creek, 1.25 mi W of Highway 140, Poinsett County, Arkansas	J. L. Harris, R. Doster
Quadrula nobilis	new	Sucarnoochee River above U.S. 11, Livingston, Sumter County, Alabama	D. Campbell, S. A. Clark
Pleurobema (*Sintoxia*) *riddellii*	186	Village Creek, Hardin County, Texas	L. Burlakova, Alex Karatayev
Pleurobema (*Sintoxia*) *rubra*	UAUC529	35.8825°N, 91.2186°W, Strawberry River 1 mi below Simstown Spring, off State Route 42, Sharp County, Arkansas	K. J. Roe *et al.*
Theliderma metanevra	new specimen	Cahaba River at Barton Beach, Perry County, Alabama	Thornhill
Toxolasma lividum	new specimen	Tennessee River mile 249, Colbert/Lauderdale County, Alabama	J. T. Garner, A. C. Suddith
Uniomerus declivis	UAUC3290	Big Sunflower River at Farrell Road Bridge, ~5 mi N of Clarksdale, Coahoma County, Mississippi	W. R. Haag, J. L. Stanton
Uniomerus tetralasmus	new specimen	32.6737°N, 87.7647°W, small creek at County Route 24, Hale County, Alabama	D. Campbell, T. Campbell
Venustaconcha pleasii	UAUC3520	Beaver Creek T25N R17W S12, Douglas County, Missouri	M. C. Barnhart
Venustaconcha pleasii	UAUC3525	Beaver Creek T25N R17W S12, Douglas County, Missouri	M. C. Barnhart

used 500 random replicates, using all the "new technology" methods (ratchet, drifting, sectorial searches, and fusing). Jackknife analyses used 500 replicates, each using a random parsimony search of 10 replicates. MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) was run for the whole data set with 2,000,000 generations, 8 chains, and sample frequency of 100; revmat, shape, pinvar, and statefreq were unlinked, and burnin was set to 5000. To test the strength of support for dividing *Pleurobema* and *Elliptio*, analyses were run including only Pleurobemini. These had 400,000 generations, 8 chains, and sample frequency of 100. Burnin was set to 1000. All of the analyses had *Elliptio sensu stricto* (*i.e.*, excluding *Eurynia* Rafinesque, 1819), *Eurynia*, *Pleurobema sensu stricto* (*i.e.*, excluding "*Pleurobema*" *collina*, "*Pleurobema*" *stabile*, *Pleuronaia gibbera*, and *Sintoxia*), and *Sintoxia* constrained individually as monophyletic. One of the analyses also specified an *Elliptio-Eurynia* clade, and another specified a *Pleurobema-Sintoxia* clade. Twice the difference in the harmonic means of the ln likelihood posterior probabilities for two different models approximates the value for the Bayes factor table of Kass and Raftery (1995) (Nylander *et al.* 2004).

RESULTS

ITS1 sequences failed to provide resolution within Pleurobemini, but they did support the exclusion of *F. ebenus* (Lea, 1831) from Pleurobemini. Although Pleurobemini as a whole and a few species-level subclades within Pleurobemini were recognizable with ITS1, most taxa formed an unresolved polytomy. In contrast, the mitochondrial genes provided good resolution.

Several clades were well-supported in the present analyses (Figs. 1–3). As in previous molecular analyses (Campbell *et al.*

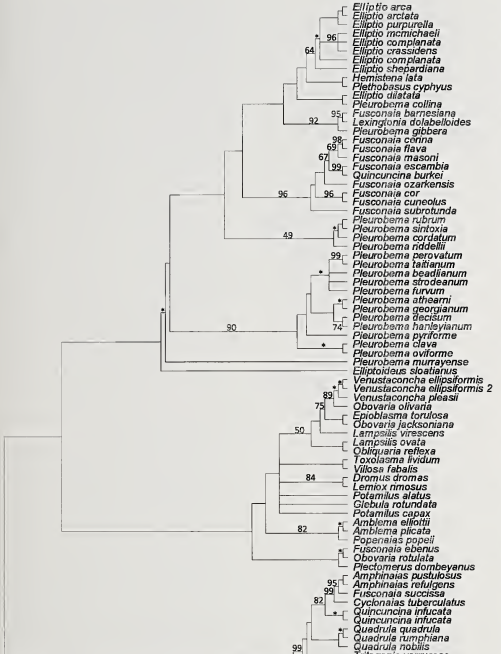

Figure 1. Strict consensus maximum parsimony tree (12 trees, length = 4647), *cox1* and *nad1* data combined. Taxa are labeled by the genera in Graf and Cummings (2007). These are the same as in Turgeon *et al.* (1998) except that *metanevra, pustulosa,* and *refulgens* were all listed as *Quadrula* in Turgeon *et al.* (1998) and both overlooked *Q. nobilis* (Conrad, 1854), recognized in Howells *et al.* (1996). Numbers on branches are jackknife percentages. * = 100% support.

2005, Campbell *et al.* 2008), Pleurobemini (*Pleurobema, Elliptio, Eurynia, Fusconaia, Hemistena, Plethobasus, Pleuronaia* Frierson, 1927, *Sintoxia* Rafinesque, 1820) was well-supported, with *Elliptoideus* Frierson, 1927 as a possible basal sister taxon. Relationships between Pleurobemini genera remain poorly-resolved. Support for most genera, including *Fusconaia*, is strong once apparently misclassified species are excluded. "*Fusconaia*" *ebenus* and "*F.*" *rotulata* are closely related to each other, but not strongly associated with any other sampled species. "*Fusconaia*" *barnesiana* (Lea, 1838) is closely related to "*Lexingtonia*" *dollabelloides* (Lea, 1840) and "*Pleurobema*" *gibberum* (Lea, 1838). "*Pleurobema*" *cordatum* (Rafinesque, 1820), "*P.*" *rubrum* (Rafinesque, 1820), and "*P.*" *sintoxia* (Rafinesque, 1820) form a clade, and "*P.*" *riddellii* is moderately supported as a member of this clade. "*Elliptio*" *dilatata* (Rafinesque, 1820), "*Pleurobema*" *stabile* (Lea, 1861), and "*Pleurobema*" *collina* place within Pleurobemini but do not strongly group with any other species.

Although the Bayesian consensus tree did not contradict a sister-taxon relationship between *Eurynia* and *Elliptio sensu stricto* and weakly supported a sister-taxon relationship between *Pleurobema sensu stricto* and *Sintoxia*, calculation of Bayes factors supports the unconstrained tree over specifying monophly of *Pleurobema* plus *Sintoxia* or *Elliptio* plus *Eurynia*. Kass and Raftery (1995) identify such values as moderately to strongly supporting the unconstrained tree; nevertheless, the Bayes factors are small compared to the differences made by changing evolutionary models (Nylander *et al.* 2004). This suggests that the criteria for "strong" support might need to be modified for phylogenetic analyses.

DISCUSSION

The presence of a few well-supported clades in a background of generally poor resolution for ITS1 suggests that it has undergone occasional purifying selection but more often has freely diverged, possibly affected by ancestral polymorphisms or hybridization. The ITS1 sequence for *Rotundaria tuberculata* (Rafinesque, 1820) includes a partial duplication of the gene region (a similar but longer partial duplication was also observed in *Strophitus undulatus* (Say, 1816) [Campbell, pers. obs.]; this would explain the

Figure 2. Strict consensus maximum parsimony tree (12 trees, length = 4647), *cox1* and *nad1* data combined. Numbers on branches are jackknife percentages. * = 100% support. Genera revised to reflect the results of the present analyses.

anomalously long fragment in White *et al.* (1996)). As the duplicate regions are not identical, independent reduction of such an ancestral polymorphism to normal length could produce a mosaic of features in the descendants.

The present data support previous molecular studies that indicate a need for revision of the genus-level classification of Pleurobemini (see also systematic taxonomy section, below) (Lydeard *et al.* 2000, Serb, Buhay *et al.* 2003, Campbell *et al.* 2005, Campbell *et al.* 2008). A few species placed in Pleurobemini belong in other tribes. "*Fusconaia*" *succissa* (Lea, 1852) belongs within Quadrulini, as do "*Quincuncina*" *infucata* (Conrad, 1834), "*Quincuncina*" *kleiniana* Lea, 1852, and "*Cyclonaias*" *tuberculatus* (Rafinesque, 1820), a result also found in part by Lydeard *et al.* (2000), Serb, Buhay *et al.* (2003) [the sequence for *C. tuberculatus* in that paper was incorrect; it was from a tissue clip received along with one for *Potamilus alatus* (Say, 1817) and evidently a mixup occurred before or after arrival at the lab], Campbell *et al.* (2005), and Williams *et al.* (2008). All four species are members of the *pustulosa* group of species in Quadrulini. Several genus- or subgenus-level names are available for this group, but the oldest turns out to be *Rotundaria* Rafinesque, 1820. Additionally, the molecular data ally *Uniomerus* with Quadrulini rather than with Pleurobemini (present study).

"*Fusconaia*" *ebenus* and "*Obovaria*" or "*Fusconaia*" *rotulata* form a distinctive clade (Lydeard *et al.* 2000, Campbell *et al.* 2005), probably also including the extinct "*Fusconaia*" *apalachicola*. Williams and Fradkin, 1999. The relationships of this clade to the rest of Ambleminae are not well-resolved. Several authors proposed that these species were closely related on morphological and anatomical grounds (Stansbery 1971, Williams and Butler 1994, Athearn 1998, Williams and Fradkin 1999, Williams *et al.* 2008). As no genus was available for this group, we propose the new genus *Reginaia* Campbell and Lydeard.

Several other taxa belong within Pleurobemini, but are not supported as members of their assigned genus. "*Pleurobema*" *collina* and "*Pleurobema*" *stabile* are clearly within Pleurobemini but not consistently associated with any other sampled taxa. The remaining species currently assigned to *Pleurobema* and *Fusconaia* form four main clades within Pleurobemini. "*Fusconaia*" *barnesiana*, "*Lexingtonia*" *dollabelloides*, and "*Pleurobema*" *gibberum* form one clade (Campbell *et al.* 2005). The genus *Pleuronaia* is available for this group (Williams *et al.* 2008). "*Pleurobema*"

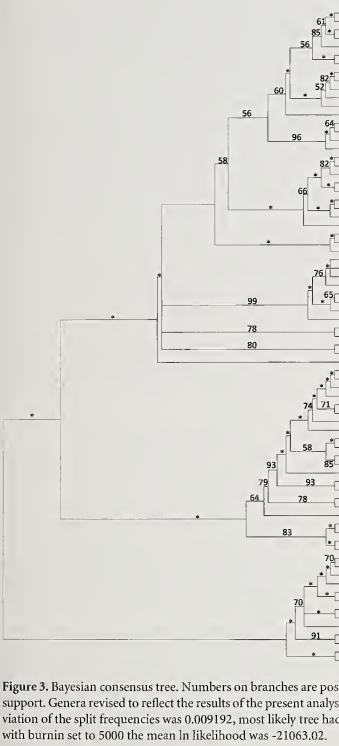

Figure 3. Bayesian consensus tree. Numbers on branches are posterior probabilities. * = 100% support. Genera revised to reflect the results of the present analyses. Final average standard deviation of the split frequencies was 0.009192, most likely tree had a ln likelihood of -21057.05, with burnin set to 5000 the mean ln likelihood was -21063.02.

cordatum, "*Pleurobema*" *sintoxia*, and "*Pleurobema*" *rubrum* form a second small clade; probable relatives include "*Pleurobema*" *riddellii* (Lea, 1862) and "*Pleurobema*" *plenum* (Lea, 1840) (Morrison *et al.* 2005, present study). This group has long been recognized on morphological and anatomical grounds (Ortmann 1918, Frierson 1927, Stansbery 1967, Watters *et al.* 2009). The genus *Sintoxia* is available for this group of species. This clade is sometimes but not consistently resolved as sister to *Pleurobema* and so might be treated as a subgenus of *Pleurobema*. The remaining species of *Pleurobema* form a large clade, including the type species of *Pleurobema*, and the remaining species of *Fusconaia* form a large clade, including the type species of *Fusconaia*, *Quincuncina*, and *Lexingtonia* (Williams *et al.* 2008). *Elliptio* also appears polyphyletic, with *E. dilatata* failing to group with other species of that genus; unpublished data suggest that a few additional species of *Elliptio* may also belong elsewhere (Serb, Bogan *et al.* 2003, McCartney and Wilbur 2007, Sommer 2007). However, the support for separating *Eurynia* and *Sintoxia* from *Elliptio* and *Pleurobema*, respectively, is relatively low, so for the present we treat these as subgenera to draw attention to their distinctiveness.

Systematic Taxonomy

Genera that have been assigned to or confused with Pleurobemini are listed below with tribe assignments.

Family Unionidae
Subfamily Ambleminae
Tribe Pleurobemini Hannibal, 1912
(= Elliptionini Modell, 1942)

Several genus-level names have been proposed for taxa in this tribe or affiliated groups. Many are from the work of Rafinesque and of Swainson, who unfortunately did not designate type species in most cases (except by monotypy or tautonomy) and often had poor descriptions and figures. Thus, determining type species requires surveying subsequent literature until the first subsequent type designation is found. Genera from Mexico, Central America, and Eurasia have also sometimes been assigned to Pleurobemini (Frierson 1927, Modell 1964, Starobogatov 1970, Nagel and Badino 2001). The relationships of Mexican and Central American unionids are poorly-known, often with no anatomical information, but biogeographically it is plausible that some might belong to Pleurobemini. As we have no new information about them, they are not listed here. No Eurasian taxa seem to be validly placed in any tribe of Ambleminae from eastern North America (Campbell *et al.* 2005, Altaba and Altaba 2009).

Genus ***Canthyria*** Swainson, 1840

Type species: *Unio spinosus* Lea, 1836 by original designation.

Considered a subjective synonym of *Elliptio* (Serb, Bogan *et al.* 2003)

Genus ***Cunicula*** Swainson, 1840

Type species: *Unio purpurascens* Lamarck, 1819 by subsequent designation (Herrmannsen 1846), a subjective synonym of *Elliptio complanata* (Lightfoot, 1786).

Considered a subjective synonym of *Elliptio* (Gangloff *et al.* in review, present analysis).

Genus ***Curricula*** Gray, 1847

Error for *Cunicula* Swainson, 1840. Gray's type designation of *Unio planulatus* Lea, 1829 would make this a subjective senior synonym of *Ptychobranchus* Simpson, 1900, but fortunately Herrmannsen's type designation of *Unio purpurascens* for the correctly spelled genus is older.

Genus ***Elliptio*** Rafinesque, 1819

Type species: *Unio* (*Elliptio*) *nigra* Rafinesque, 1820 (a subjective synonym of *Elliptio crassidens* (Lamarck, 1819)) by subsequent designation (Ortmann 1912). Simpson (1900) listed *crassidens* as the type, not a valid designation as it was not an originally included species.

Other included taxa in this study: *E. arca* (Conrad, 1834), *E. arctata* (Conrad, 1834), *Elliptio complanata* (Lightfoot, 1786), *Elliptio mcmichaeli* Clench and Turner, 1956, *Elliptio pullata* (Lea, 1856), *Elliptio purpurella* (Lea, 1857), and *Elliptio shepardiana* (Lea, 1834).

Taxa excluded from *Elliptio sensu stricto*: *Elliptio* (*Eurynia*) *dilatata* (Rafinesque, 1820)

Genus ***Elliptoideus*** Frierson, 1927

Type species: *Unio sloatianus* Lea, 1840, by original designation.

Other included taxa: none

The relationships of this genus to Pleurobemini are not very strongly supported. Further study is desirable.

Genus ***Ensinaia*** Starobogatov, 1970

Type species: *Unio sheppardianus* [sic] Lea, 1834, error for *Elliptio shepardiana* (Lea, 1834), by original designation.

Considered a subjective synonym of *Elliptio* (Gangloff *et al.* in review, Morrison *et al.* 2005, present results).

Genus ***Eurynia*** Rafinesque, 1819

Type species: *Unio dilatata* Rafinesque, 1820, by subsequent designation in Herrmannsen (1847).

Other included taxa: none

Agassiz (1852) overlooked Herrmannsen's type designations for several taxa and used *Eurynia* for the group now called *Ligumia*. His usage was followed by several other authors. More confusion comes from the many misspellings: Vokes (1980) lists *Eurinea*, *Euryma*, *Eurynaia*, *Eurynea*, and *Rurynea*. Although *Elliptio* (*Eurynia*) *dilatata* has generally been placed in *Elliptio* on morphological and anatomical grounds (Ortmann and Walker 1922a), molecular studies consistently fail to group it with *Elliptio* and weakly associate it with other taxa instead (Campbell *et al.* 2005, Campbell *et al.* 2008, McCartney and Wilbur 2007, Gangloff *et al.* in review).

The shell is more elongate than most species of *Elliptio sensu stricto*, but some Atlantic drainage species are also elongate and might be related to *Elliptio* (*Eurynia*) *dilatata* rather than to *Elliptio crassidens*. *Elliptio arca*, from the Mobile basin, is very similar conchologically to *Elliptio* (*Eurynia*) *dilatata*, but molecular data place *Elliptio arca* with *Elliptio crassidens*.

Genus ***Fusconaia*** Simpson, 1900

Type species: *Unio trigonus* Lea, 1831 (a subjective synonym of *Fusconaia flava* (Rafinesque, 1820)) by original designation.

Other included taxa in this study: *Fusconaia burkei* (Walker, 1922), *Fusconaia cerina* (Conrad, 1838), *Fusconaia cor* (Conrad, 1834), *Fusconaia cuneolus* (I. Lea, 1840), *Fusconaia escambia* Clench and Turner, 1956, *Fusconaia masoni* (Conrad, 1834), *Fusconaia ozarkensis* (Call, 1887), and *Fusconaia subrotunda* (I. Lea, 1831).

Taxa excluded from *Fusconaia*: *Reginaia ebenus* (Lea, 1831), *Reginaia rotulata* (B. H. Wright, 1899), *Reginaia apalachicola* (Williams and Fradkin, 1999), *Rotundaria succinea* (Lea, 1852), and *Pleuronaia barnesiana* (Lea, 1838).

Genus ***Hemilastena*** Agassiz, 1852

Invalid emendation of *Hemistena* Rafinesque, 1820.

Genus ***Hemistena*** Rafinesque, 1820

Type species: *Anodonta* (*Lastena*) *lata* Rafinesque, 1820 by monotypy.

Other included taxa: none

Genus ***Lexingtonia*** Ortmann, 1914

Type species: *Unio subplanus* Conrad, 1837 by original designation.

Considered a subjective synonym of *Fusconaia*. Williams *et al.* (2008) report that molecular data indicate that *L. subplana* is a synonym of *F. masoni*, and present data indicate that *F. masoni* belongs in *Fusconaia*.

Genus ***Lintoxia*** "Rafinesque, 1820"

Error for *Sintoxia* Rafinesque, 1820. Cited in Vokes (1980), as not seen; presumably a typographical error in one of his sources. Now listed in several nomenclatural compilations. Also purportedly altered to *Lyntoxia* by Agassiz (1846), an error for *Syntoxia*, an invalid emendation actually present in Agassiz.

Genus ***Luteacarnea*** Frierson, 1927–1929?

Type species: *Unio cooperianus* Lea, 1834, designated herein. *Luteacarnea* is a replacement name for *Striata* Frierson, 1927. The originally designated type species was *Obovaria striata* Rafinesque, 1820, which Frierson (1927) regarded as a senior synonym of *Unio cooperianus*, a usage followed by some other authors. However, Parmalee and Bogan (1998), Williams *et al.* (2008), and Watters *et al.* (2009) identified *O. striata* as a synonym of *Obovaria subrotunda* Rafinesque, 1820. Given the uncertainty about the identity of *Obovaria striata*, we believe it would best promote stability in nomenclature to unambiguously associate the genus with the species Frierson had in mind. Therefore, we designate *U. cooperianus* as the type species of *Luteacarnea* under article 70.3 of the ICZN Code (ICZN 1999).

Although Haas (1969b) and Modell (1964) place this genus in Quadrulini, current classification treats it as a subjective synonym of *Plethobasus*. We obtained an ITS1 sequence that supports its inclusion in Pleurobemini but does not provide clear evidence of its affinities within the tribe; attempted amplification of other genes has not been successful.

This name was proposed as a replacement name for *Striata* Frierson, 1927 in the corrigenda to Frierson (1927). The absence of the corrigenda in many copies and its apparently arbitrary placement either at the front or the back of the book indicate that it was not a part of the original publication. Unfortunately, there are no indications in the corrigenda of when it was published, and the publisher's records were lost in a flood years ago (Carey C. Newman, pers. comm.). Because it seems to have been issued separately from the main text, the corrigenda seems to qualify as a separate publication, but its date of publication is unclear. The first published reference to names in the corrigenda that we have located is Strecker (1929), who lists the names from the corrigenda as if they were a part of the original and does not explicitly reference the corrigenda as a separate item (the cited pagination in Strecker (1929) does not mention it). This suggests that the corrigendum was published fairly closely with the original, as does the fact that the typeface matches (one copy seen had a typewritten copy of the corrigenda, presumably added by a later owner). This and the other genera from the corrigenda to Frierson (1927) have sometimes been credited to Thiele, 1934, presumably by authors who lacked access to the corrigenda and so were unable to find the genus in Frierson's work.

Genus ***Obliquata*** Frierson, 1927

Type species: *Obliquaria* (*Scalenaria*) *obliquata* Rafinesque, 1820 (a subjective synonym of *Sintoxia rubra* Rafinesque, 1820), by original designation.

Considered a subjective synonym of *Sintoxia* Rafinesque, 1820.

Genus ***Odatelia*** Rafinesque, 1832

Type species: *Odatelia radiata* Rafinesque, 1832, by monotypy (other species listed as synonyms); a subjective synonym of *Hemistena lata* (Rafinesque, 1820).

Considered a subjective synonym of *Hemistena*.

Genus ***Plethobasus*** Simpson, 1900

Type species: *Unio aesopus* Green, 1827 (a subjective synonym of *Plethobasus cyphus* (Rafinesque, 1820))

Other included taxa: *Plethobasus cicatricosus* (Say, 1829), *Plethobasus cooperianus* (Lea, 1834). Both of these species are highly imperiled and no definitive molecular data are available; however, the strong morphological similarities make their placement in *Plethobasus* very likely.

Genus ***Pleurobema*** Rafinesque, 1819

Type species: *Unio mytiloides* Rafinesque, 1820 by subsequent designation (Herrmannsen 1847) (a subjective synonym of *Pleurobema clava* (Lamarck, 1819))

Other included taxa in this study:

Pleurobema athearni Gangloff *et al.*, 2006, *Pleurobema beadlianum* (Lea, 1861), *Pleurobema decisum* (Lea, 1831), *Pleurobema furvum* (Conrad, 1834), *Pleurobema georgianum* (Lea, 1841), *Pleurobema hanleyianum* (Lea, 1852), *Pleurobema oviforme* (Conrad, 1834), *Pleurobema perovatum* (Conrad, 1834), *Pleurobema pyriforme* (Lea, 1857), *Pleurobema strodeanum* (Wright, 1898), and *Pleurobema taitianum* (Lea, 1834).

Taxa excluded from *Pleurobema sensu stricto*: "*Pleurobema*" *collina* (Conrad, 1837), *P.* (*Sintoxia*) *cordatum* (Rafinesque, 1820), *Pleuronaia gibbera* (Lea, 1838), *P.* (*Sintoxia*) *plenum* (Lea, 1840), *P.* (*Sintoxia*) *riddellii* (Lea, 1862), *P.* (*Sintoxia*) *rubrum* (Rafinesque,

1820), and *P.* (*Sintoxia*) *sintoxia* (Rafinesque, 1820). "*Pleurobema*" *stabile* (Lea, 1861) is not consistently supported as a member of the genus, but not consistently excluded, either.

Genus ***Pleuronaia*** Frierson, 1927

Type species: *Unio barnesianus* Lea, 1838 by original designation

Other included taxa: *Pleuronaia gibbera* (Lea, 1838), *Pleuronaia dolabelloides* (Lea, 1840) (Williams *et al.* 2008).

Nomenclatural note: Frierson also misspelled this name as *Pleuronia*. We select *Pleuronaia* as having priority over *Pleuronia* because the spelling *Pleuronia* occurs only once in Frierson (1927), because the *-naia* ending is common in unionids, and because *Pleuronaia* is the spelling used by subsequent authors.

Genus ***Quincuncina*** Ortmann, 1922 in Ortmann and Walker (1922b)

Type species: *Quincuncina burkei* Walker, 1922, by original designation.

Ortmann and Walker (1922b) established the genus because of the distinctive sculpture of the type species. However, previous (Lydeard *et al.* 2000, Serb, Buhay *et al.* 2003, Campbell *et al.* 2005) and present molecular data, in addition to the close anatomical similarity (Williams *et al.* 2008), indicate that *burkei* belongs in *Fusconaia*. "*Quincuncina*" *infucata* (Conrad, 1834) and "*Quincuncina*" *kleiniana* (Lea, 1852) belong in the *pustulosa* group of *Quadrula* (Serb, Buhay *et al.* 2003, Williams *et al.* 2008, present data). The affinities of "*Quincuncina*" *mitchelli* (Simpson, 1895) are unknown; it may be extinct (Burlakova *et al.* 2011).

This genus is considered a junior subjective synonym of *Fusconaia* (Williams *et al.* 2008).

Genus ***Sayunio*** de Gregorio, 1914

Type species: *Unio dehiscens oriensopsis* de Gregorio, 1914 (a subjective synonym of *Hemistena lata* (Rafinesque, 1820)) by original designation.

Considered a subjective synonym of *Hemistena*.

Genus ***Scalenaria*** Rafinesque, 1820

Type species: *Obliquaria* (*Scalenaria*) *scalenia* Rafinesque, 1820 (a subjective synonym of *Pleurobema clava* (Lamarck, 1819)), by subsequent designation (Herrmannsen 1848)

Considered a subjective synonym of *Pleurobema*.

Genus ***Sintoxia*** Rafinesque, 1820

Type species: *Obliquaria sintoxia* Rafinesque, 1820, by tautonomy.

Other included taxa: *Sintoxia cordata* (Rafinesque, 1820), *Sintoxia plena* (Lea, 1840), *Sintoxia riddellii* (Lea, 1862), *Sintoxia rubra* (Rafinesque, 1820). The *cordatum* group has been widely recognized (*e.g.*, Ortmann 1918, Frierson 1927, Stansbery 1967), but there is much uncertainty about the number of species. Frierson (1927) assigned *Sintoxia riddellii* to this group, but most other studies have focused on the Mississippi drainage taxa. It may not be monophyletic (Burdick and White 2007, Morrison *et al.* 2005). Some analyses place it close to *Pleurobema*, so we currently treat it as a subgenus rather than a genus. *Syntoxia* is an unjustified emendation.

Genus ***Striata*** Frierson, 1927

Type species: *Unio cooperianus* Lea, 1834, designated herein. The originally designated type species was *Obovaria striata* Rafinesque, 1820, but the identity of Rafinesque's species is debated. This genus name is a junior homonym and was replaced with *Luteacarnea* Frierson, 1927–1929? See further discussion under *Luteacarnea*. We designate *Unio cooperianus* as the type species of *Striata* under article 70.3 of the ICZN Code. *Striata* Frierson is a junior subjective synonym of *Plethobasus*.

Tribe uncertain

(This includes poorly-characterized names as well as well-studied taxa that are not clearly affiliated with a named tribe)

Genus ***Aximedia*** Rafinesque, 1820

Type species: Rafinesque (1820) included three new species: *Unio* (*Aximedia*) *elliptica* Rafinesque, 1820; *U.* (*A.*) *levigata* Rafinesque (1820) (he also suggested it might instead belong in *Obliquaria* (*Plagiola*) Rafinesque, 1820); and *U.* (*A.*) *zonalis* Rafinesque, 1820. No type species has been selected in the literature that we have examined. *U. elliptica* is considered a synonym of *Pleurobema clava* by Parmalee and Bogan (1998); *U. levigata* is considered a synonym of *Obovaria subrotunda* by Parmalee and Bogan (1998) and *U. zonalis* is considered a synonym of *Obovaria subrotunda* by Haas (1969a). Since *Pleurobema* applies to *P. clava*, whereas the precise relationship of *Obovaria subrotunda* to *O. retusa*, the type of *Obovaria*, is unknown, it might be more useful to have *Aximedia* apply to *levigata* or *zonalis*. We leave formal type designation for someone doing a revision of the *Obovaria-Epioblasma-Venustaconcha* clade.

Genus ***Bariosta*** Rafinesque, 1831

Type species: *Unio ponderosus* Rafinesque, 1831, by subsequent designation (Frierson 1914). Williams *et al.* (2008) cite Fischer (1886) as designating a type;

however, Fischer sometimes identified the cited species in his descriptions as the type and sometimes just as an example. In his list of unionid generic names, he does not specify whether the species cited are types or examples, and taking them to be types would disrupt existing usage for *Toxolasma* and possibly other genera. Although Frierson (1914) thought that *Unio ponderosus* was recognizable as *Plectomerus dombeyanus* (Valenciennes, 1827; Frierson cited *Unio trapezoides* Lea, 1831, a subjective synonym of *dombeyanus*), other authors have not agreed. Williams *et al.* (2008) declared *Unio ponderosus* and *Bariosta* to be *nomina dubia* and *Bariosta* to be a *nomen oblitum*.

Genus ***Flexiplis*** Rafinesque, 1831

Type species: *Anodonta digonata* Rafinesque, 1831, by monotypy.

Haas (1969b) synonymized *Flexiplis* with *Hemistena*, but the identity of *A. digonata* is highly doubtful (even differing in Haas 1969a). Williams *et al.* (2008) declared *Flexiplis* and *Anodonta digonata* to be *nomina dubia* and *Flexiplis* to be a *nomen oblitum*.

Genus ***Popenaias*** Frierson, 1927

Type species: *Unio popeii* Lea, 1857 by original designation

Other included taxa: Additional species in Mexico and Central America have been assigned to *Popenaias* (Graf and Cummings 2007), but they have not been available for molecular studies. *Elliptio buckleyi* (Lea, 1843) was placed with *Popenaias* by Heard and Guckert (1971) based on the breeding season, but all other data place it with *Elliptio*, including molecular data (Gangloff *et al.* in review). Chapman, Gordon *et al.* (2008) found that *Popenaias* is closely related to Lampsilini.

Genus ***Reginaia*** Campbell and Lydeard, new genus

Type species: *Unio ebenus* Lea, 1831

Other included species: *Reginaia rotulata* (Wright, 1899), *Reginaia apalachicola* (Williams and Fradkin, 1999). *Reginaia apalachicola* is assigned to this genus on morphological grounds; it is known only from prehistoric middens.

Diagnosis: Shell relatively oval, unsculptured; beaks strong and anterior; posterior slope rounded, with a weaker posterior ridge than in *Fusconaia* (Fig. 4). Periostracum dark, especially in mature individuals, without rays, unlike most *Fusconaia*. Very distinct based on molecular data (Lydeard *et al.* 2000, Serb, Buhay *et al.* 2003, Campbell *et al.* 2005, Burdick and White 2007, Campbell and Lydeard 2012, present data), not clearly assignable to any recognized tribe. The shell is rounded posteroventrally, whereas typical *Fusconaia* has a well-developed posterior ridge producing an angle at the posteroventral end (less well-developed in *F. subrotunda*). Beaks are less anterior in most true *Fusconaia* than in *Reginaia* (*F. cor* and *F. subrotunda* may have similarly anterior beaks). Umbonal cavity in *Reginaia* deep and compressed; in *Fusconaia* beak cavities less compressed. *Fusconaia* often has a small accessory anterior

Figure 4. *Reginaia ebenus* (Lea, 1831), the type species of *Reginaia* n. gen. (University of Rochester 13524 from "Ohio", now in Paleontological Research Institution collections). Scale bar in cm.

Table 3. Bayes factors. "Constraint" is what group was constrained as monophyletic. "Mean ln likelihood" is the harmonic mean of the likelihood values (excluding burnin). The Bayes factor table uses twice the difference between the likelihoods for the models being compared (in this case, between the unconstrained and constrained trees). In this case, it indicates the degree to which the unconstrained model is favored over the one with the constraint. A value of 6 to 10 is strong support, over 10 is very strong support (Kass and Raftery 1995, Nylander *et al.* 2004).

Constraint	Mean ln likelihood	2*ln (Bayes factor)
Unconstrained	-9574.26	not applicable
Elliptio + *Eurynia*	-9576.56	4.6
Pleurobema + *Sintoxia*	-9577.60	6.68

pseudocardinal which we have not observed in *Reginaia*. The conglutinate tends to fragment, unlike most *Fusconaia* (Barnhart *et al.* 2008). Differs from Lampsilini and Pleurobemini except for *Fusconaia* in being tetragenous. The *Pleurobema* (*Sintoxia*) group can resemble *Reginaia* in shell form, but they have a flattened area or sulcus in front of the posterior ridge and are ectogenous.

Etymology: Conflation of *regina*, a queen, and *naias*, a nymph, commonly used as a designation for the pearly freshwater mussels. "*Regina*" reflects the common name of ebonyshell for *ebenus* and pigtoe for *Fusconaia* and refers to the Empress of Blandings, a fictional prize black pig (Wodehouse 1927).

Genus ***Uniopsis*** Swainson, 1840

Type species: *Uniopsis mytiloides* Swainson, 1840 by monotypy. Identity uncertain.

Swainson initially identified the species as *Uniopsis radiata* in part I of his work. Swainson's footnote suggests that his specimen might be "*Margaritana radiata* of Lea's Synopsis", but Swainson admitted that this identification was a guess based only on the species name. This is a rather cryptic reference to *Alasmodonta radiata* Conrad, 1834 (now *Anodontoides radiatus*). In part II, Swainson renames it *Uniopsis mytiloïdes* [the umlaut is now omitted in accord with the modern ICZN code (ICZN 1999)]. Presumably the change of species name in part II of Swainson reflected a decision that it wasn't *radiata* of Lea's list. Swainson confused things further by mentioning a conspecific (or possibly congeneric; he calls it "of this type") specimen that had been labeled "*Alasmodon inflata*". We have not located any plausible source for this name and assume it was a manuscript name; published unionoid species named "*inflata*" or "*inflatus*" before 1840 are clearly not similar.

Swainson's figure is somewhat similar to elongate *Pleurobema* species such as *Pleurobema clava* (a senior synonym of *Unio mytiloides* Rafinesque, 1820), but Swainson said it had no lateral teeth. The color pattern of fine radial lines in his figure (if accurate) is also atypical for *Pleurobema*. The lack of pseudolaterals and Swainson's assignment of the genus to "Alasmodontinae" [sic] have generally suggested some species of *Alasmidonta* or a related genus to most authors.

Simpson (1900) identified *Uniopsis mytiloides* as a synonym of *Alasmidonta undulata* Say, 1816, and most authors have followed this identification. However, Modell (1964) listed the genus as a synonym of *Pleurobema*. This probably is based on identification of *Uniopsis mytiloides* as a new genus assignment for *Unio mytiloides* Rafinesque, 1820 rather than as a new species of Swainson's. That interpretation is very unlikely, because Swainson assigned *Unio mytiloides* Rafinesque to *Unio sensu stricto* both in part I and part II of his work (he used *Unio* for *Pleurobema* and placed true *Unio* in another genus). Instead, it seems most likely that Swainson named his new species after Rafinesque's, because he thought that *Uniopsis* was an alasmidontine analogue of "*Unio*". Watters *et al.* (2009) question Simpson's identification and instead suggest that Swainson had a non-North American specimen. Thus, the identity of *Uniopsis* is unsettled, but it is unlikely to belong in Pleurobemini.

Tribe Quadrulini Ihering, 1901

Genus ***Cyclonaias*** Pilsbry in Ortmann and Walker, 1922a

Type species: *Obliquaria* (*Rotundaria*) *tuberculata* Rafinesque, 1820, by original designation.

Some authors have placed this genus in Pleurobemini based on its usually ectobranchous brooding; however, it otherwise closely resembles other Quadrulini. This is an objective synonym of *Rotundaria*.

Genus ***Rotundaria*** Rafinesque, 1820

Type species: *Obliquaria* (*Rotundaria*) *tuberculata* Rafinesque, 1820, by subsequent designation (Valenciennes 1827).

Following Agassiz (1852), many workers used *Rotundaria* for *Cyclonaias tuberculatus* (e.g., Simpson 1900, 1914, Ortmann 1920, Modell 1949). Ortmann and Walker (1922a) pointed out that Herrmannsen (1848) had designated *Obliquaria* (*Rotundaria*) *subrotunda* Rafinesque, 1820 as the type of *Rotundaria*, although they ignored other type designations in Herrmannsen (1846–1852). Therefore, they created *Cyclonaias* Pilsbry in Ortmann and Walker, 1922a as a replacement name for *Rotundaria sensu* Agassiz. But there is an older type designation for *Rotundaria*, in Valenciennes (1827), who stated that Rafinesque had sent a lot of *tuberculatus* to the museum in Paris as the type of the new genus *Rotundaria* ("comme le type d'un nouveau genre qu'il nomme *Rotundaria*", p. 231). This also makes the well-known "*Cyclonaias*" *tuberculatus* the type of this genus, whereas the next-oldest genus name for the "*Quadrula*" *pustulosa* (Lea, 1831) group, *Amphinaias*, is based on the poorly-known and probably extinct *Unio couchianus* Lea, 1860 from the Rio Grande system.

The "*Quadrula pustulosa*" group has been widely recognized on conchological grounds (Simpson 1914, Frierson 1927, Serb, Buhay *et al.* 2003, Graf and Cummings 2007, Watters *et al.* 2009). It includes species with a relatively round shell, in contrast to the squarer shells of the *Q. quadrula* (Rafinesque, 1820) group and the strong posterior ridge of the "*Q*". *metanevra* (Rafinesque, 1820) group or the elongate shape of *Tritogonia* Agassiz, 1852. Most individuals have nodes, as typical for quadrulines, but they do not have the large, projecting knobs of many other quadrulines. The only reasons for separating "*Cyclonaias*" *tuberculatus* from the *pustulosa*

group are the usually ectobranchous brooding and the coppery-purple nacre (Ortmann and Walker 1922a). Although the pattern of gill use in brooding is an important feature in unionoid classification, no one feature (including DNA) is immune to convergence, and the report of partial tetrabranchy in *tuberculatus* (Frierson, 1927) suggests that not much weight should be placed on ectobranchy in this case. Previous molecular data has supported recognition of the *pustulosa* group (Serb, Buhay *et al.* 2003). The host-attraction and glochidial release patterns vary somewhat between the groups of Quadrulini (Barnhart *et al.* 2008), but better documentation for more species is needed to confirm the generality of these patterns.

We follow Graf and Cummings (2007) in treating this group as a separate genus, although it could also be treated as a subgenus of a broadly defined *Quadrula*. Watters *et al.* (2009) also suggest recognizing the *pustulosa* group as a distinct genus but do not identify a suitable genus name.

Subsequent subjective or objective synonyms include *Amphinaias* Fischer and Crosse, 1894 (type species, *Unio couchianus* Lea, 1860 by original designation), which is the genus used in Graf and Cummings 2007; *Cyclonaias* Pilsbry, 1922 (type species, *Obliquaria (Rotundaria) tuberculata* Rafinesque, 1820 by original designation); *Bullata* Frierson, 1927 (type species, *Unio pustulosus* Lea, 1831 by original designation; invalid--a junior homonym of the marginellid gastropod genus *Bullata* Jousseaume, 1875); and *Pustulosa* Frierson, 1927–1929? (type species, *Unio pustulosus* Lea, 1831 by original designation).

Rotundaria tuberculata often uses only the outer gills for brooding, which has led some authors to place it in Pleurobemini (Graf and Cummings 2007); however, shell morphology, other anatomy (Williams *et al.* 2008), and molecular data (present results) place it in Quadrulini.

Genus ***Theliderma*** Swainson, 1840

Type species: *Obliquaria* (*Quadrula*) *metanevra* Rafinesque, 1820 by subsequent designation (as *metanera* [*sic*]), Gray (1847) (other misspellings include *metanerva*, *metaneurus*, *metanever*, and *metaniver*). This is a subjective senior synonym of *Orthonymus* Agassiz, 1852 (type species, *Unio cylindricus* Say, 1817, original designation). Simpson (1900, 1914) treated *metanevra* as the type of *Quadrula* and used *Theliderma* for *Quadrula sensu stricto*, but his type designation for *Quadrula* is invalid (the type of *Quadrula* is *Obliquaria* (*Quadrula*) *quadrula* Rafinesque, 1820 by tautonomy) and for *Theliderma* Simpson's designation is well subsequent to Gray. *Theliderma* was used by Graf and Cummings (2007), and *Orthonymus* was treated as a valid genus for the *metanevra* group by authors such as Modell (1964) and Davis and Fuller (1981). The present discussion is mainly intended to explain the discrepancy with Simpson's usage. Molecular data (Serb, Buhay *et al.* 2003) as well as morphological data (Simpson 1914, Graf and Cummings 2007) support this as a distinct group.

Genus ***Uniomerus*** Conrad, 1853

Type species: *Unio declivis* Say, 1831 (subsequent designation, Frierson 1927, 1927–1929?). Earlier designations of *Unio tetralasmus* (Say, 1831) as the type fall afoul of the fact that Conrad failed to include that species in the original description, though he did include some subjective synonyms of it. Frierson (1927–1929?) indicated that the species listed on p. 9–11 of Frierson (1927) were the types of the respective genera, thus making his mention of *U. declivis* a type designation.

Other included taxa: *Uniomerus carolinensis* (Bosc, 1801), *Uniomerus columbensis* (Lea, 1857), *Uniomerus tetralasmus* (Say, 1831).

Although morphological and anatomical studies have generally placed *Uniomerus* in Pleurobemini, molecular data place it in Quadrulini. Some species of *Uniomerus* are easily confused with *Elliptio*, but *Uniomerus* almost always can be recognized by the two parallel grooves on the posterior side of the posterior ridge.

Tribe Lampsilini Ihering, 1901

Genus ***Lastena*** Rafinesque, 1820

Type species: *Anodonta* (*Lastena*) *ohiensis* Rafinesque, 1820, by subsequent designation (Herrmannsen 1847), now placed in *Potamilus* Rafinesque, 1818.

This genus was occasionally used for *Hemistena lata* (based on a later type designation) or *Utterbackia imbecilis* (Say, 1829) (based on misidentification of *ohiensis*) by earlier authors. Considered a subjective synonym of *Potamilus*.

Genus ***Lostena*** Gray, 1847

Error for *Lastena* Rafinesque, 1820.

Genus ***Obovaria*** Rafinesque, 1819

Type species: *Unio retusa* Lamarck, 1819, by ICZN Opinion 2188 (ICZN 2008).

Prevalent usage reflected the incorrect assumption that *Obovaria retusa* Rafinesque, 1819 was the same as *Unio retusa* Lamarck, 1819, but in fact Rafinesque was unaware of Lamarck's work at the time (Bogan *et al.* 2006). The type designation of *Obovaria* in Herrmannsen (1847) made *Obovaria obovalis* Rafinesque, 1820 the type of the genus. Agassiz (1852) selected *O. torsa* Rafinesque, 1820, a subjective synonym of *Unio retusa* Lamarck, as type, a designation followed by several authors (Simpson 1900, Ortmann and

Walker 1922a [though aware of Herrmannsen's designation], Modell 1964). *Obovaria obovalis* is widely recognized as a neglected senior synonym of *Unio ebenus* Lea, 1831 (Say 1834, Williams *et al.* 2008). However, current usage of *Obovaria* and *ebenus* are so well established that there seems little point in re-establishing Rafinesque's names in this group. The ICZN (2008) designated *Unio retusa* Lamarck, 1819 as the type of *Obovaria* and made *Obovaria obovalis* a *nomen oblitum* (Opinion 2188 2008). This follows traditional usage, but *Obovaria retusa* is on the brink of extinction and no molecular data are yet available, making it somewhat inconvenient as the type of the genus. Anatomically, *O. retusa* is similar to other species currently assigned to *Obovaria* (Ortmann 1912, Williams *et al.* 2008). Molecular data (Campbell *et al.* 2005, Zanatta and Murphy 2006, present results) indicate that "*Obovaria*" *olivaria* (Rafinesque, 1820) is relatively distinct from other *Obovaria* and may be closer to *Venustaconcha*. This suggests that greater weight should be given to the anatomical and conchological differences that prompted Simpson (1900) to propose *Pseudoon* for *olivaria*, and suggests that there may be unappreciated variation within *Obovaria*. (Note: the sequences identified in Campbell *et al.* (2005) as *Venustaconcha pleasii* Marsh, 1891 are in fact *V. ellipsiformis* (Lea, 1838); the *cox1* sequence AY655025 from Campbell *et al.* (2005) labeled as *Venustaconcha ellipsiformis* is a *Ptychobranchus*). Watters *et al.* (2009) refer to *O. subrotunda* as the type of *Obovaria* in their etymology, perhaps a lapse for its being the species Herrmannsen designated as type of *Rotundaria*. They identify *retusa* as the type under "Type species".

Genus ***Pseudoon*** Simpson, 1900

Type species: *Unio ellipsis* Lea, 1828 (a subjective synonym of *Obovaria olivaria* (Rafinesque, 1820)) by original designation. Simpson spelled it *Pseudoön*, but diacritical marks are not allowed under current ICZN rules (ICZN 1999).

Ortmann (1912) claimed that *Obovaria castanea* (Lea, 1831), a primary homonym now known as *O. jacksoniana* (Frierson, 1912), was intermediate between *Pseudoon* and standard *Obovaria* in anatomy, but for taxa sampled so far, *O. jacksoniana* seems to closely match other *Obovaria* in DNA (Campbell *et al.* 2005). *Pseudoon* is confusingly similar in spelling to *Pseudodon* Gould, 1844, an Asian unionid genus. Further study of the *Epioblasma-Obovaria-Venustaconcha* clade may support its recognition as a full genus; we use it as a subgenus here to draw attention to the apparent difference between *olivaria* and the rest of *Obovaria*. *Pseudoon* is neuter, so the species would become *Pseudoon olivarium*.

Genus ***Stenelasma*** Herrmannsen, 1849.

Invalid emendation of *Lastena* Rafinesque, 1820.

SUMMARY

Past and present molecular data suggest that several groups of unionid species do not match currently recognized genera. Several genus names in the literature, currently treated as subjective synonyms, are available, but their identity is often obscure or unclear. A review of available genera in Pleurobemini and taxa that have been assigned to Pleurobemini results in several nomenclatural changes. The type species of *Quincuncina* and *Lexingtonia* place within *Fusconaia*. *Eurynia*, *Sintoxia*, *Pleuronaia*, and *Rotundaria* deserve recognition as subgenera or genera based on molecular, conchological, and anatomical features; new genera will probably be needed for some additional taxa such as *Pleurobema collina*.

Within Pleurobemini, three previously synonymized genera are recognized. *Eurynia* applies to "*Elliptio*" *dilatata*. *Sintoxia* is the oldest available subgenus for the "*Pleurobema*" *cordatum* group (*cordatum*, *plenum*, *riddellii*, *rubrum*, *sintoxia*). *Pleuronaia* includes "*Fusconaia*" *barnesiana* (Lea, 1838), "*Lexingtonia*" *dolabelloides* (Lea, 1840), and "*Pleurobema*" *gibberum* (Lea, 1838). Several species currently assigned to Pleurobemini are removed from the tribe; many also require nomenclatural changes. *Fusconaia apalachicola*, *F. ebenus*, and *F. rotulata* receive the new genus *Reginaia* herein. *Reginaia* is not clearly associated with any particular tribe within Ambleminae. *Fusconaia succissa*, *Cyclonaias tuberculatus*, and the *Quincuncina infucata* complex belong in the "*Quadrula*" *pustulosa* group. A convoluted nomenclatural history restores *Rotundaria* as the oldest genus name for the *pustulosa* group. *Uniomerus* also shows molecular affinity to Quadrulini rather than Pleurobemini.

ACKNOWLEDGMENTS

In addition to the authors, C. R. Dean, Q. Parham, K. K. Small, J. Serb, J. Moseley, and A. Wethington helped with lab work; K. K. Small and Q. Parham were supported as Hughes Undergraduate Research Interns by a Howard Hughes Medical Institute Undergraduate Biological Sciences Education Program grant to The University of Alabama. Many people provided specimens; they are acknowledged in Table 2. These include tissue samples from Virginia Tech and Auburn University Museum collections. The ABI 3100 automated sequencer was funded by a NSF equipment grant to C. Lydeard, R. Mayden, M. Powell, and P. Harris (DBI-0070351). A grant from the U.S. Fish and Wildlife Service to C. Lydeard supported this work. The TNT program is available with the sponsorship of the Willi Hennig Society. The paper was completed as part of Lydeard's Independent Research and Development at NSF. The views in this paper are those of the authors and not of NSF. The reviewers and editors suggested several improvements to the text of the paper.

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Submitted: 8 July 2010; **accepted:** 4 July 2011;
final revisions received: 18 November 2011